LITERATURE CITED

AGASHE, S. N. 1964. The extra-xylary tissues in certain calamites from the American Carboniferous. Phytomorphology **14**: 598–611.

ESAU, K., V. I. CHEADLE, and E. GIFFORD, JR. 1953. Comparative structure and possible trends of specialization of the phloem. Amer. J. Bot. **49**: 9–19.

GOLUB, S. J. and R. H. WETMORE. 1948. Studies of development in the vegetative shoot of Equisetum arvense, II. The mature shoot. Amer. J. Bot. **35**: 767–781.

JOHNSON, M. A. 1933. Origin and developmen of tissues in Equisetum scirpoides. Bot. Gaz. **94**: 469–494.

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A New Genus of Salviniaceae and a New Species of Azolla from the late Cretaceous[1]

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The Salviniaceae are represented in the Cretaceous by two species of *Azolla* recently described from North America. *Azolla cretacea* Stanley is based on massulae; it has been reported from the Hell Creek Formation of South Dakota (Stanley, 1965), Montana (Norton and Hall, 1967) and the time-equivalent Edmonton Formation of Alberta (Srivastava, 1966). *Azolla geneseana* Hills and Weiner is known both as massulae and megaspores from the Edmonton Formation in Alberta (Hills and Weiner, 1965).

These few reports are scarcely indicative of the place of the family in the Cretaceous, at least in the fluviatile deposits of eastern Montana that I have looked at. By using the simple sieving and sorting techniques customarily used for isolating megaspores from sediments, large numbers of massulae and megaspores of *Azolla* have been found. They are so abundant and heterogeneous as to suggest that the family was not only a conspicuous component of the aquatic vegetation, but was morphologically

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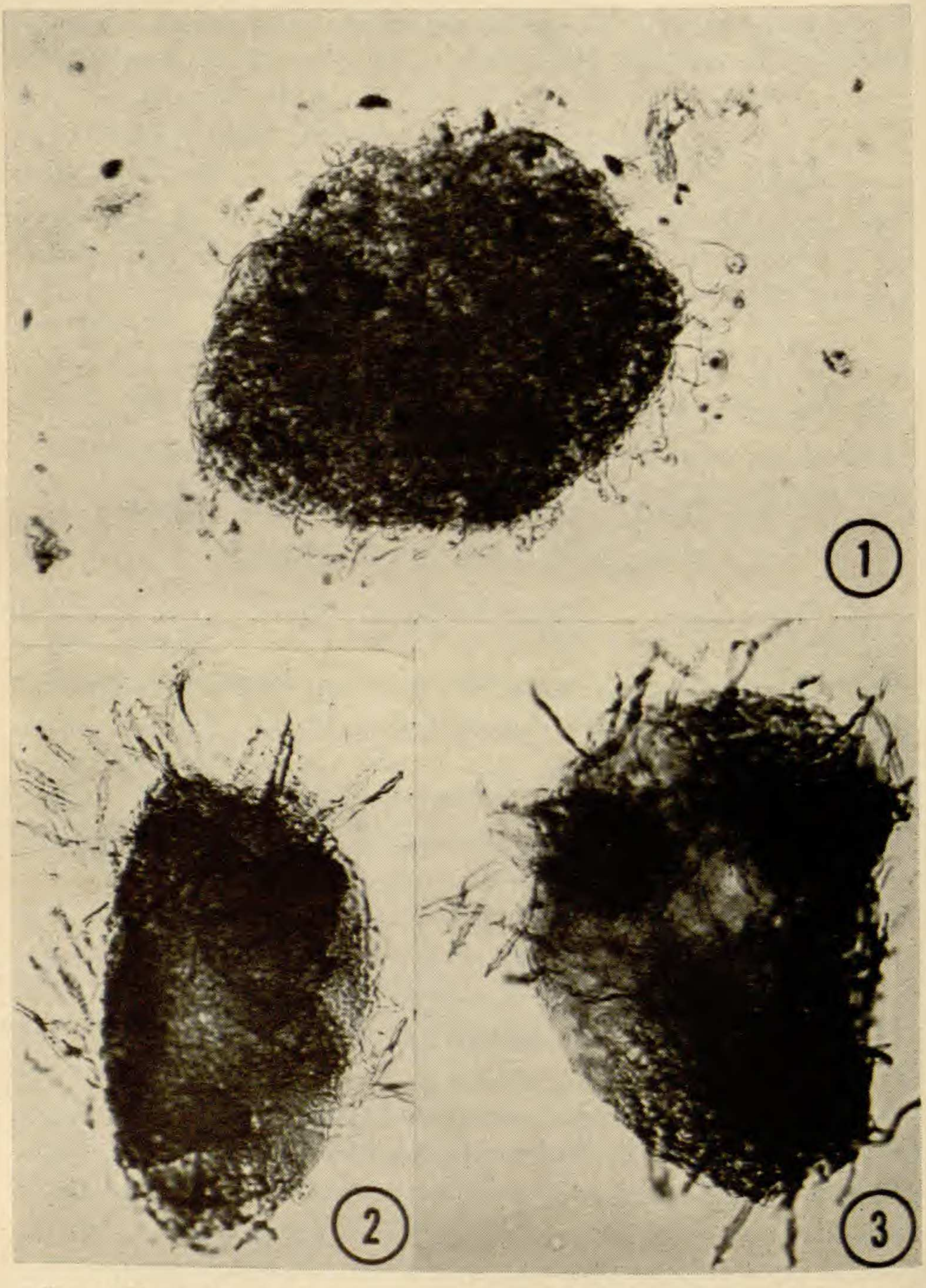


FIG. 1. HOLOTYPE OF AZOLLA CIRCINATA, × 325. FIGS. 2 AND 3. MASSULAE FROM THE PARATYPE OF AZOLLOPSIS TOMENTOSA, ×175.

more diverse then than it has been subsequently. One new genus, with both megaspores and massulae, and a new species of *Azolla* representing what I consider to be a new section of the genus are described here.

Among the extant species of *Azolla*, as well as the previously described fossils, there are two types of massulae. Section *Azolla* accomodates those species whose massulae have anchor-shaped glochidia; in sect. *Rhizosperma* the massulae lack glochidia. Section *Azolla* dates from the Cretaceous and sect. *Rhizosperma* from the Oligocene. The massulae of the species of *Azolla* described here possess glochidia that are filamentous and coiled.

AZOLLA sect. **Filifera** J. W. Hall, sect. nov.

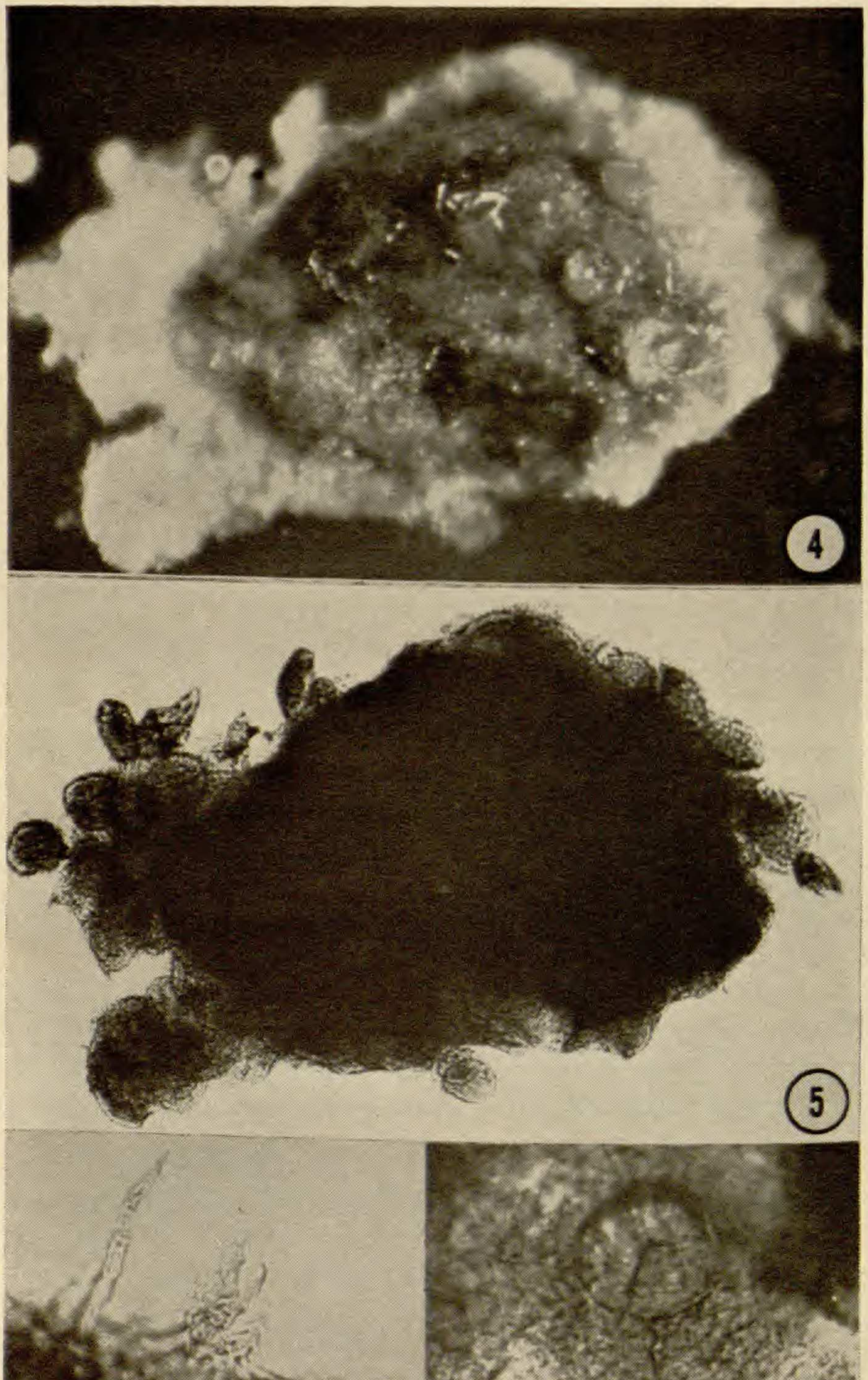
Massulae with long, slender, hairlike or filamentous, non-septate glochidia. Glochidia tips equal in diameter to the distal portions of the glochidia and lacking terminal structural differentiation, slightly enlarged or inflated, or coiled. Megaspores and vegetative remains unknown.

TYPE: *Azolla circinata* Oltz & Hall.

Section *Filifera* includes massulae with glochidia which tend to resemble the perisporal hairs on the body of many *Azolla* megaspores, both living and fossil. Although megaspores with coiled perisporal hairs or with hairs having enlarged tips have not been reported, they do occur in some of the Cretaceous deposits which I have examined; furthermore, there are massulae with straight, unbranched glochidia in some of these deposits. All of these await further, detailed study before their relationships and taxonomy can be clarified. My present opinion is that this section is primitive in *Azolla* because glochidia and megaspore ornamentation are only slightly, if at all, different.

AZOLLA **circinata** Oltz & Hall, sp. nov.

Massulae nearly circular to oval in outline, ca. 100–175 μ in longest dimension, 75–150 μ in shortest dimension, the surface often marked with wide, rugulo-reticulate thickenings, these sometimes circular and overlapping, giving the massulae a foamy aspect. Glochidia numerous, 1–2 μ wide, up to ca. 15 μ long, usually not extended greatly beyond the margin of the massula proper, variously coiled at the apex, some appearing merely inflated at the tip, usually with 1 gyre, or sometimes with only a



AZOLLOPSIS COCCOIDES

partial gyre. Microspores small, often completely obscured by the plasmodium of the massula, 20–24 μ in diam., probably psilate and thin-walled. Megaspores and vegetative remains unknown.

TYPE: Slide HH 16, coordinates 38.6 × 105.2, reference 48.0 × 122.1 (paleobotanical collections, MIN), from the Hell Creek Formation (Maestrichtian) near the center of S16, T25N, R43E, McCone Country, Montana. *Fig. 1.*

Azollopsis J. W. Hall, gen. nov.

Megaspore apparatus with a conspicuous, tomentose perispore and a spherical, trilete endospore. Numerous float-like structures imbedded in or attached to the hairs of the perispore. Massulae with few microspores and conspicuous multi-hooked or barbed glochidia. Vegetative remains unknown.

TYPE: *Azollopsis coccoides* J. W. Hall.

The long, tortuous but otherwise unstructured hairs of the perispore are like those on the megaspores of species of *Azolla*, but the mass of them is greater than in that genus. The floats are relatively small, very numerous, and scattered throughout the hairs of the perispore or attached to them at the surface of the spore. The number, size, and position of the floats serves to distinguish *Azollopsis* from *Azolla*, as do the barbed glochidia of the massulae.

AZOLLOPSIS **coccoides** J. W. Hall, sp. nov.

Megaspore apparatus spherical to oval, as in the genus, 560–990 μ (aver. 706 μ) overall[2]; megaspore walls finely foveolate, 6–9 μ thick. Floats very numerous, 40–90 μ (aver. 72 μ) in diam., circular in outline, disk-shaped, sculptured as in *A. tomentosa.*

Massulae attached to the megaspore, ca. 120 μ in diam.,[3] with only 2 or 3 spores each, these circular, 44–50 μ (aver. 47 μ) in diam., with laesurae extending to the equator, the surface

[2] Intact endospores could not be measured because all are obscured by the tomentose perispore.

[3] The exact limits were mostly obscured because the massulae were deeply imbedded in perisporal hairs and merged with the floats.

FIG. 4. HOLOTYPE IN REFLECTED LIGHT, × 90. FIG. 5. SAME, IN TRANSMITTED LIGHT, × 90. FIG. 6. GLOCHIDIA FROM A MASSULA OF THE PARATYPE, × 400. FIG. 7. MICROSPORE IN MASSULA FROM THE PARATYPE, × 400.

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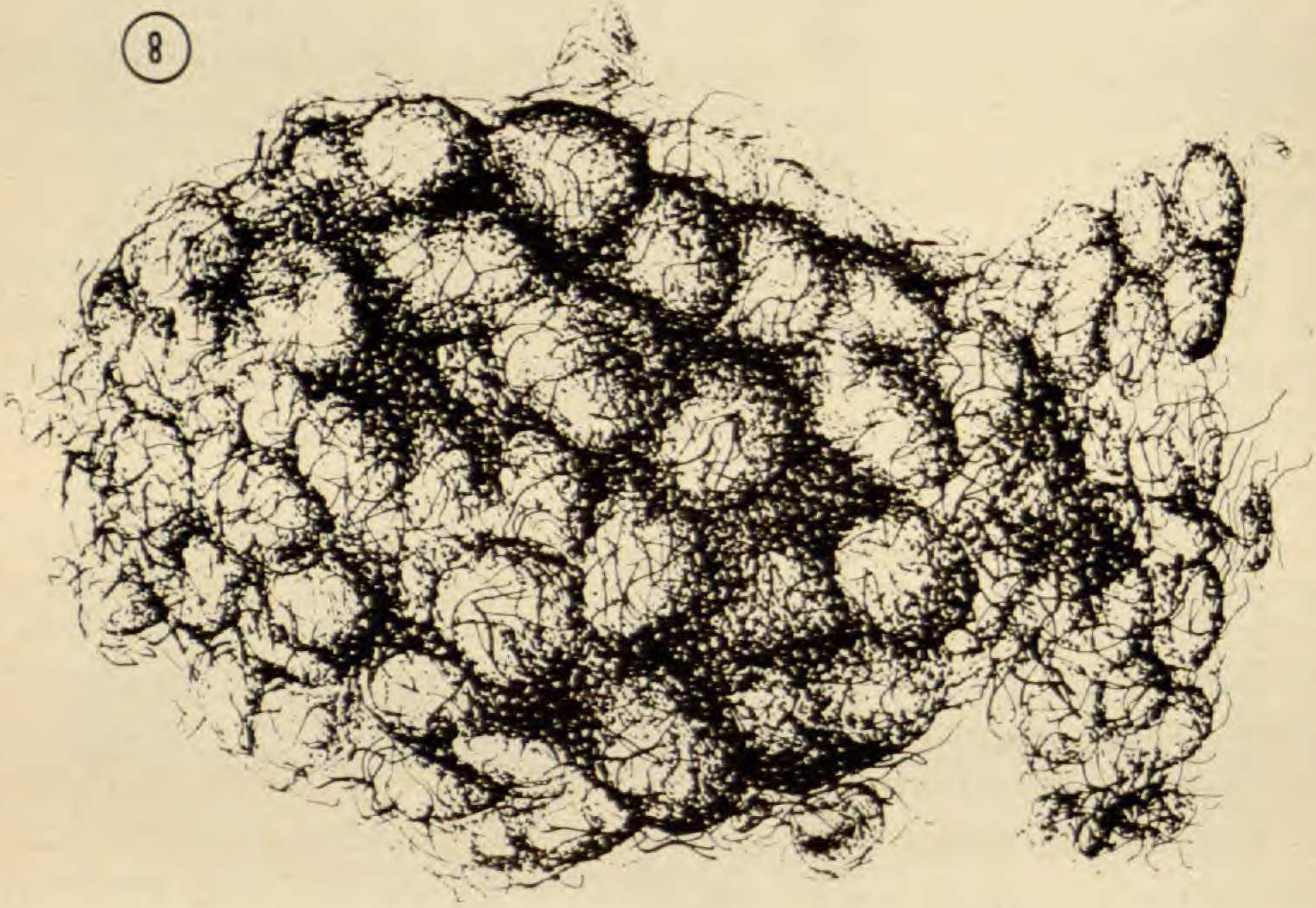

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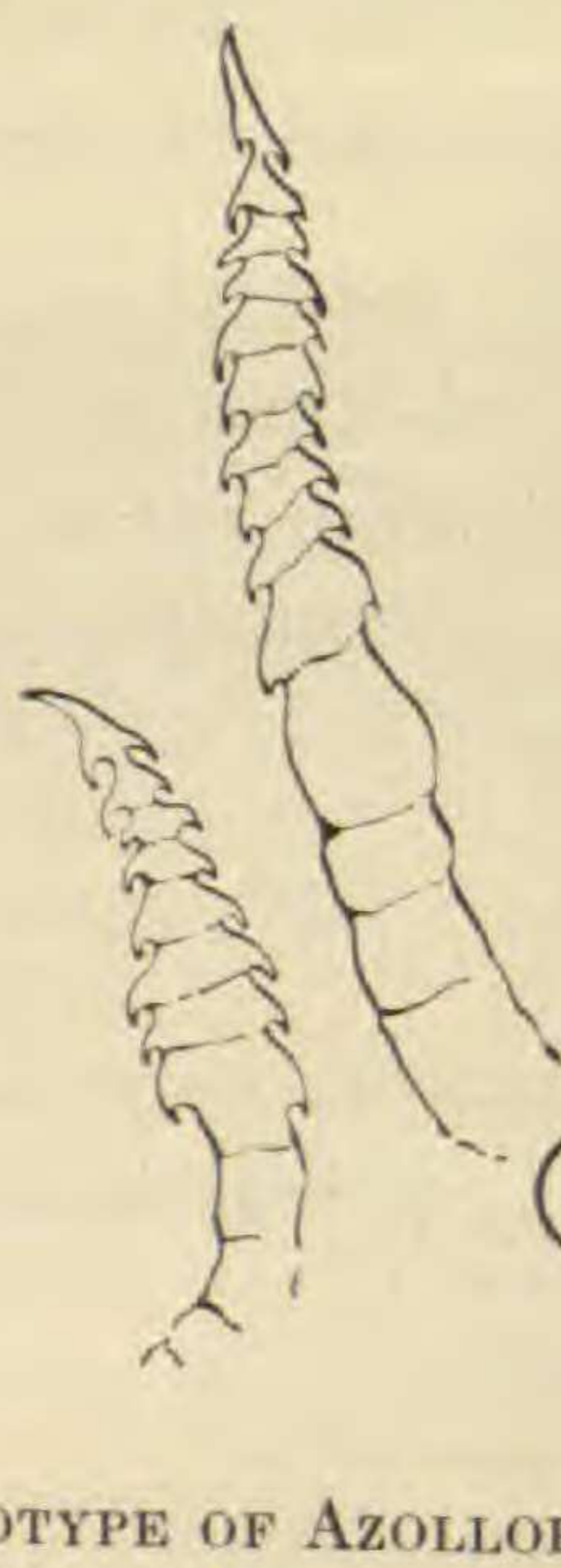

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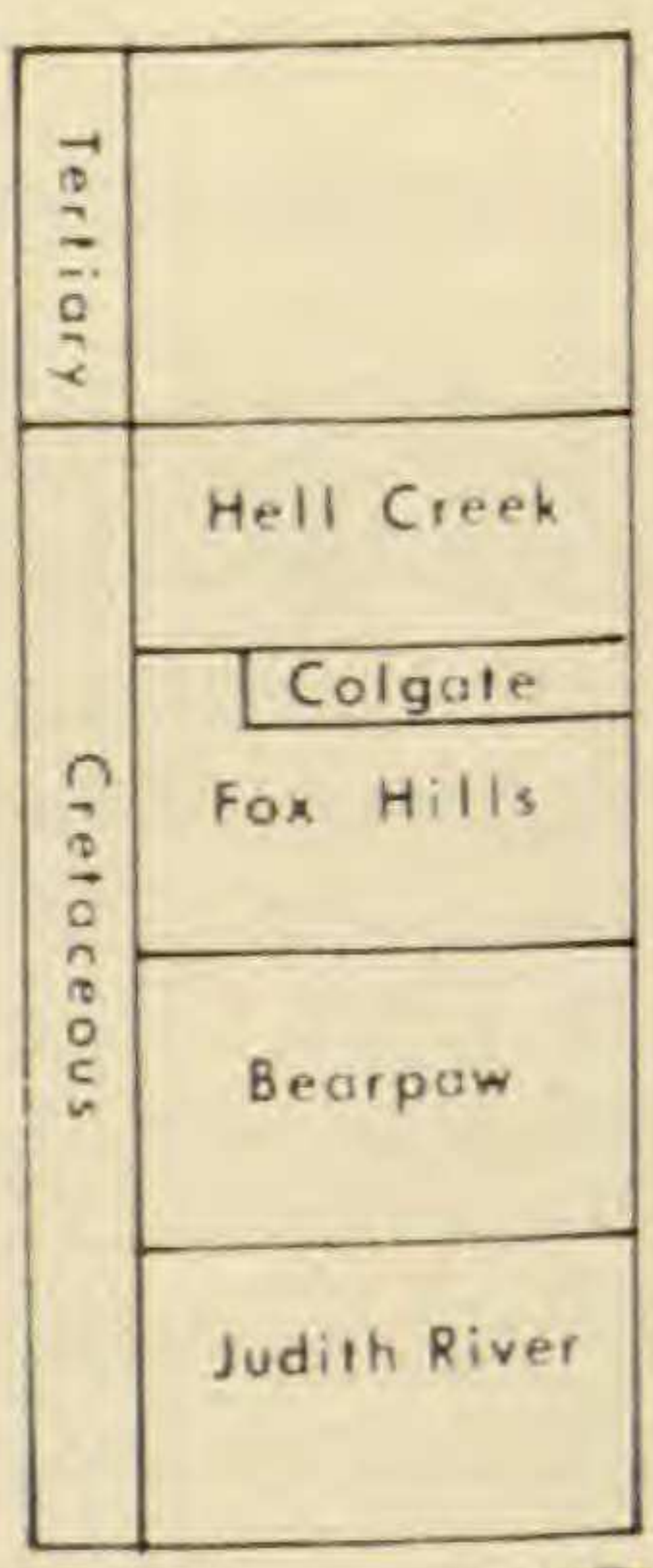

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Fig. 8. Drawing of the holotype of Azollopsis coccoides (cf. Figs. 4 and 5), × 90. Fig. 9. Glochidia of Azollopsis tomentosa (cf. fig. 12), × 450. Fig. 10. Glochidia of A. coccoides (cf. Fig. 6), ×900. Fig. 11. Diagram of stratigraphic column in eastern Montana showing relative position of formations in which Azolla circinata and Azollopsis spp. occur.

probably psilate and the wall 1–2 μ thick. Glochidia numerous, barbed, distinctly septate, 2–5 μ wide, with 6–15 barbs arranged in 2 rows, each glochidial "cell" with 2 opposite barbs.

TYPE: Slide 223–3 (paleobotanical collections, MIN), from the Judith River Formation, Upper Cretaceous (Campanian), at the west end of the Fort Peck Reservoir at the "Robinson Bridge," Philips County, Montana. *Figs. 4, 5, 8,* and *10.*

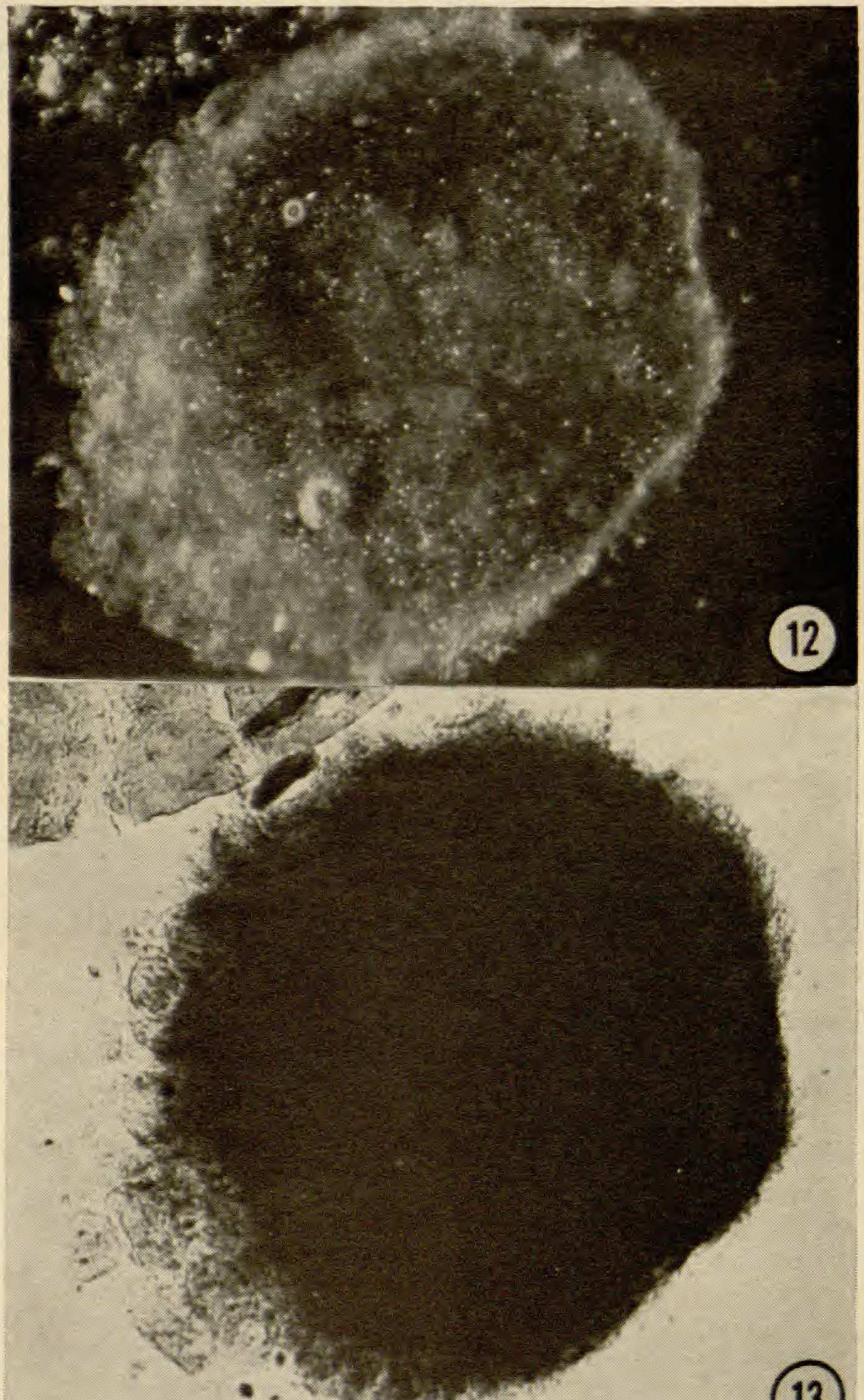
PARATYPE: Slide 223–1, coordinates 134.8 × 51, reference 131.8 × 72.3 (paleobotanical collections, MIN). Locality as for the holotype. *Figs. 6, 7,* and *10.*

The holotype possesses both megaspores and massulae, but the glochidia of the latter are seen to better advantage in the paratype. Except for the slightly larger dimensions, which may not be significant because of the smaller number of specimens seen, the megaspores of this species are virtually identical to those of *Azollopsis tomentosa*; the differences between the two species are in the massulae. The only massulae seen were those attached to the megaspores, and every megaspore had several massulae attached. The apparent effectiveness of their attachment, to the extent that they are surrounded by floats and perisporal hairs, contrasts sharply with their lack of attachment in *A. tomentosa*. Compared with that species, *A. coccoides* has fewer spores per massula, laesurae extending to the spore equator, narrower, distinctly septate glochidia with numerous barbs, and smaller massulae.

AZOLLOPSIS **tomentosa** J. W. Hall, sp. nov.

Megaspore apparatus spherical to oval,[4] as in the genus, 462–924 μ (aver. 680 μ) overall; endospores 400–480 μ (aver. 430 μ) in diam. Megaspore surface foveolate, sometimes slightly scabrate to psilate, the wall 6–8 μ thick. Floats numerous, ca. 60 μ in diam., circular in outline, but sometimes oblate in side view and disk-shaped rather than spherical, the surface composed of irregularly arranged granules and rods, sometimes vaguely reticulate and with the vacuolate aspect found in the floats of species of *Azolla*. Floats occurring only at the periphery of the perispore and extending

[4] The latter shape is due to the greater mass of floats and perisporal hairs at one end of the spore; it cannot be determined whether this is the distal or proximal end because laesurae are not often seen.



Holotype of Azollopsis tomentosa

beyond its margin or completely surrounded by the tomentose hairs.

Massulae variable in size and shape, mostly oval to subcircular, occasionally elliptical or reniform, 146 × 215 μ to 245 × 630 μ, mostly between 200 × 250 μ and 200 × 300 μ. Surface of the massulae with numerous, septate or non-septate glochidia ca. 60–90 μ long, 6–10 μ wide, each with 4–6 retrorse barbs, one of these terminal. Microspores usually 4–8 (sometimes 12) per massula, 25–50 μ in diam., probably psilate, with short laesurae.

TYPE: Slide 208–11, coordinates 59.6 × 139.1, reference 67.8 × 132.8 (paleobotanical collections, MIN), from the Colgate member, Fox Hills Sandstone, Upper Cretaceous (Maestrichtian), in S16, T13N, R55E, Dawson County, Montana. *Figs. 12* and *13*.

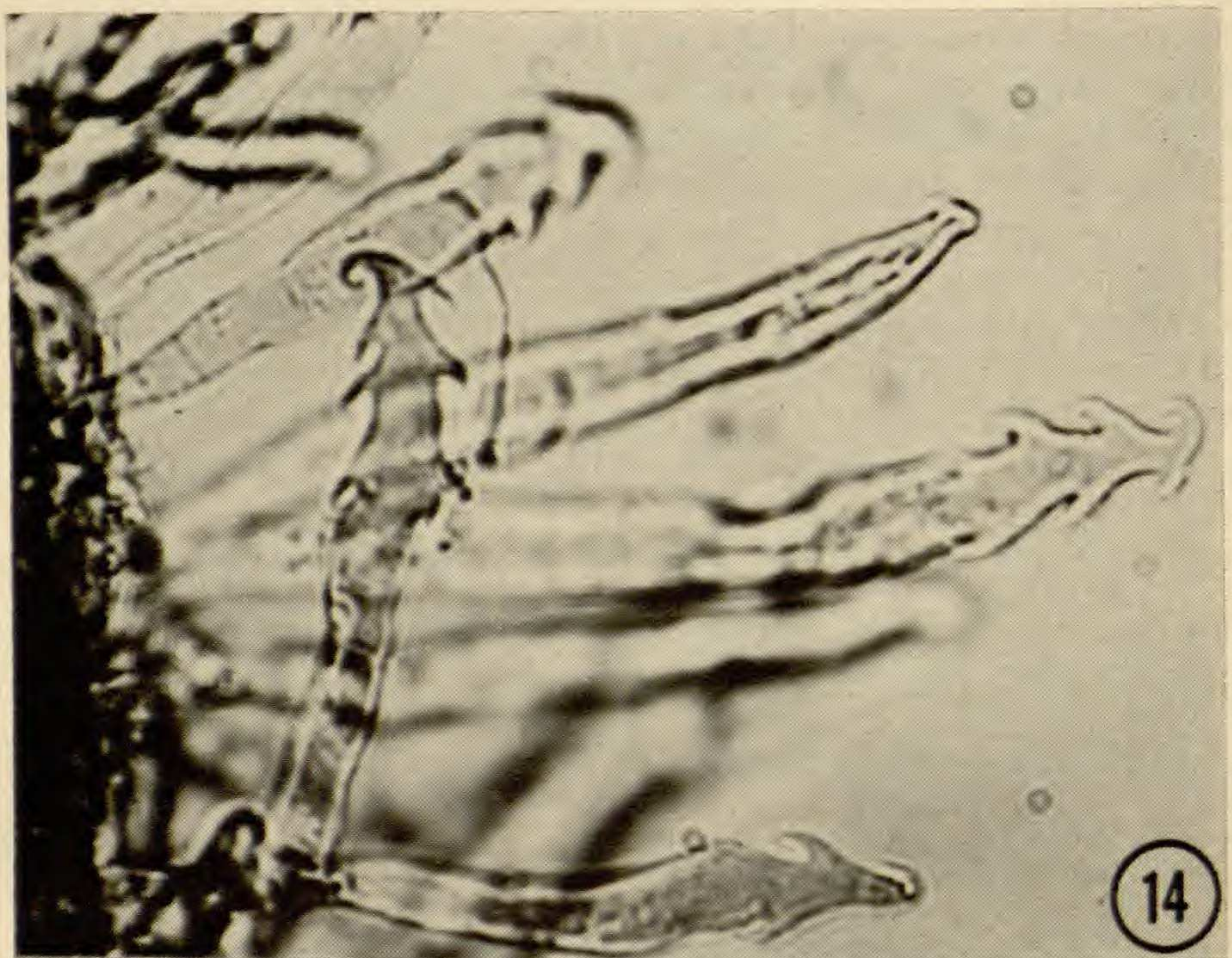
PARATYPES: Slide 208–1, coordinates 38.0 × 124.5, reference 12.1 × 119.5 (*Fig. 2*) and coordinates 35.8 × 125.4, reference 12.1 × 119.5 (*Fig. 3*) (both paleobotanical collections, MIN). Locality as for the holotype.

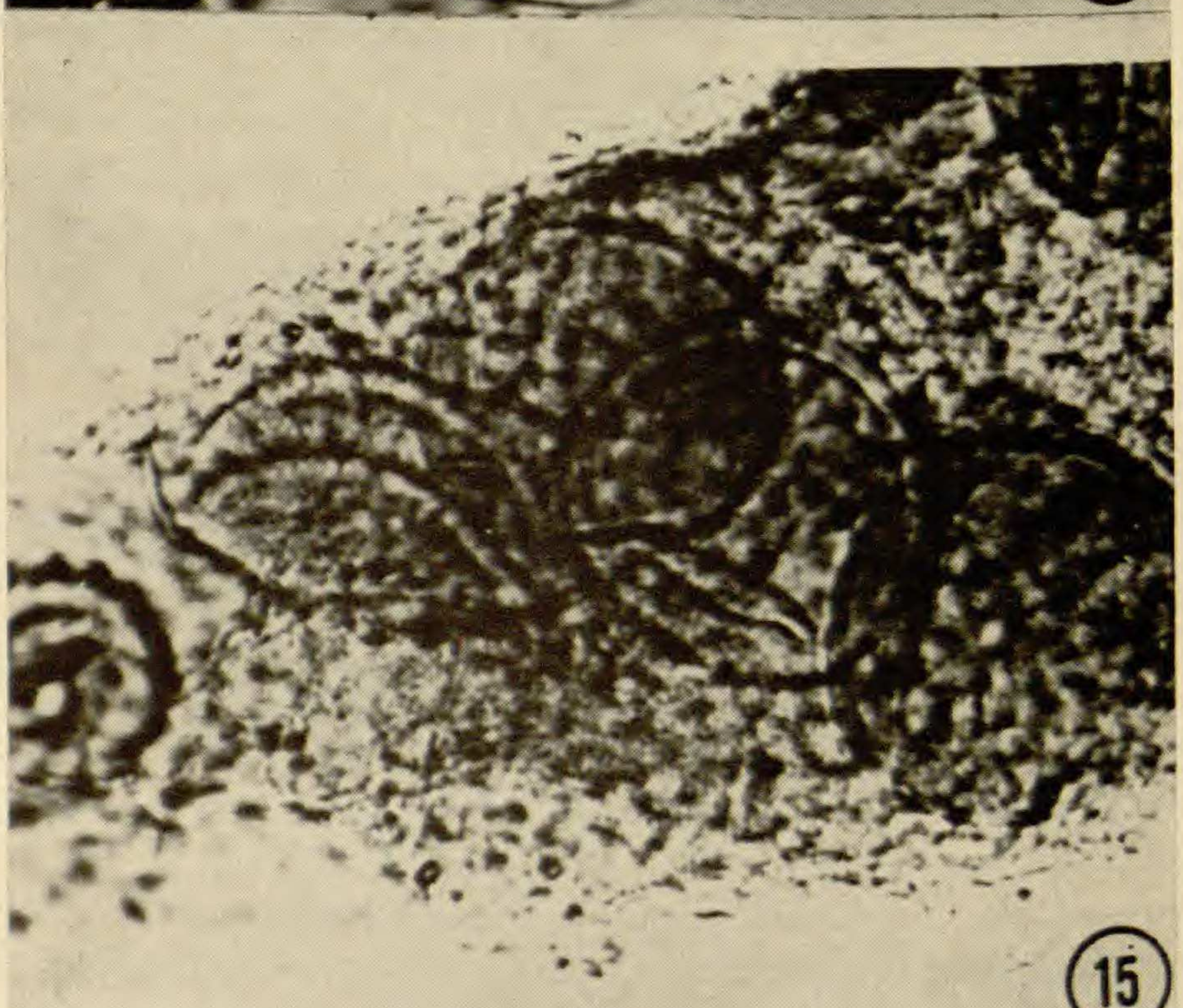
The massulae of this species are extremely large; some of them approach the size of megaspores. None has been found attached to the megaspores, but this may be due to their being dislodged during preparation. The glochidia are stouter in this species than in *A. coccoides*, are less conspicuously septate, and have fewer barbs.

DISCUSSION

The term "float" is applied to the spherical objects in the perispore of the megaspore apparatus of *Azollopsis* in deference to its use in *Azolla*, although in that genus, as has been pointed out by many authors, the term is a misnomer, for the megaspores sink shortly after being shed. Whether this was also the case in *Azollopsis* will never be known, but, at least superficially, the so-called floats seem to increase the surface area. They are not hollow, and any supportive function would have come from their numerous vacuolar cavities. Those floats that cling to the periphery of the megaspore resemble small, glochidia-less massulae, and it was my first impression that this was actually what they

FIG. 12. MEGASPORE IN REFLECTED LIGHT, × 100. FIG. 13. SAME, IN TRANSMITTED LIGHT, × 100.





Azollopsis tomentosa

were. However, there are several reasons why they cannot be massulae, the most important being the lack of microspores; another is their presence deep among the perisporal hairs, where it is unlikely that a massula would be able to penetrate; and a third, of course, is the occurrence of massulae with barbed glochidia actually attached to the megaspore in *A. coccoides.* If one can attribute to *Azollopsis* the kind of ontogenetic development of the megaspore and its swimming apparatus of *Azolla,* then the position of the floats, their large number, and their structure may be explained readily.

In the development of the megasporangium of *Azolla* there are 32 spores, separated by a periplasmodium derived from the tapetum of the sporangium, and all but one spore aborts (Eames, 1936, p. 250). The periplasmodium and abortive spores fill the upper part of the sporangium, above the developing megaspore; three vacuoles appear in the plasmodial mass, the degenerating nuclei are distributed into each vacuolar region, and a float develops from each. The developing megaspore also lies in a vacuole filled with a cytoplasmic fluid that becomes granulate. This cytoplasm develops into a foamy meshwork, and a perispore is formed, having a structure similar to that of the floats. Perisporal hairs then develop over the surface of the perispore; these seem homologous with glochidia. A float is the homologue of a massula.

Only a slight departure from this pattern would produce the numerous floats of *Azollopsis.* If, instead of aggregating apically, the aborting spores remained scattered around the developing megaspore, and if each aborting spore developed in association with a small periplasmodial mass, the situation in *Azollopsis* would arise. Furthermore, if the development of floats occurred just prior to the formation of perisporal hairs (as in *Azolla*), many of the floats would then be surrounded by hairs. This presumed developmental pattern is somewhat like that for the development of the massulae, with microspores, in *Azolla.* Since massulae and floats are homologous in that genus, they probably are in *Azollopsis*

FIG. 14. SEPTATE AND NON-SEPTATE GLOCHIDIA (CF. FIGS. 1 AND 2), × 1045.
FIG. 15. MICROSPORES IN MASSULA, × 1045.

as well; the resemblance of floats to glochidia-less massulae is not difficult to imagine.

The Judith River Formation, in Montana, is stratigraphically below any horizon from which remains of the Salviniaceae have been recovered until now. It lies in the Campanian stage of the European sequence; the Colgate Member, Fox Hills Sandstone is younger, and is in the Maestrichtian stage. *Fig. 11* shows the stratigraphic relationships of the formations involved. The fluvial Judith River sediments were covered by a transgressing Bearpaw sea; when this regressed, the Fox Hills Sandstone was deposited; the Colgate Member is its uppermost, most shoreward phase. The Hell Creek Formation is again fluvial. *Azollopsis* must have occupied a non-marine refugium during Bearpaw and Fox Hills times, and then moved eastward, as the evolved species *A. tomentosa*, by Colgate times. The record of other pollen and spore types is not yet well enough known to substantiate this suggestion, but the small mammals apparently do. There are generic, but not specific, similarities in small mammals in the Judith River and Hell Creek formations (A. Sahni and R. E. Sloan, pers. comm.). Additional examples demonstrating species evolution in the floras of these two formations can thus be expected.

LITERATURE CITED

EAMES, A. J. 1936. Morphology of Vascular Plants. Lower Groups. IX + 433 pp. McGraw-Hill, N.Y.

HILLS, L. and N. WEINER. 1965. Azolla geneseana n. sp. and revision of Azolla primaeva. Micropaleontology **11**(2): 255–261.

NORTON, N. J. and J. W. HALL. 1967. Guide Sporomorphae in the Late Cretaceous—Early Tertiary of Eastern Montana (U.S.A.). Review of Palaeobotany and Palynology. **2**: 99–110.

SRIVASTAVA, S. K. 1966. Upper Cretaceous microflora (Maestrichtian) from Scollard, Alberta, Canada. Pollen et Spores **8**(3): 497–552.

STANLEY, E. A. 1965. Upper Cretaceous and Paleocene plant microfossils and Paleocene Dinoflagellates and Hystrichospherids from northwestern South Dakota. Bull. Amer. Paleontol. **49**(222): 175–384.

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